Food for thought: supplementary feeding as a driver of ecological change in avian populations

Food for thought: supplementary feeding as a driver of ecological change in avian populations

Gillian N Robb[1], Robbie A McDonald[2], Dan E Chamberlain[3], and Stuart Bearhop[1,4*]

Every year, millions of households provide huge quantities of supplementary food to wild birds. While alteration of the natural dynamics of food supply represents a major intervention in avian ecology, we have a remarkably limited understanding of the impacts of this widespread pastime. Here, we examine the many and varied responses of birds to supplementary feeding at backyard feeders – in large-scale management projects and in focused academic studies – and evaluate population responses to the bird-feeding phenomenon. Our review encompasses a wide range of species, from songbirds to raptors, and compares provisioning with a variety of foods, at different times of year and in different locations. We consider positive impacts, such as aiding species conservation programs, and negative ones, such as increased risk of disease transmission. It seems highly likely that natural selection is being artificially perturbed, as feeding influences almost every aspect of bird ecology, including reproduction, behavior, demography, and distribution. As the effects of bird feeding cascade through ecosystems and interact with processes of environmental change, we suggest areas for future research and highlight the need for large-scale experiments, with a particular focus on the backyards of an increasingly urban and generous, but sometimes fickle, human population.

Front Ecol Environ 2008; 6(9): 476–484, doi:10.1890/060152

The popularity of bird feeding has increased rapidly in the past few decades. Up to 43% of households in the US regularly feed birds (Martinson and Flashpoler 2003), while in the UK, this figure is close to 75% (Cowie and Hinsely 1988). Food availability is clearly one of the main factors limiting bird populations, and supplementary feeding reduces the risk of starvation and may enhance reproductive performance (Newton 1998). Despite the impressive scale of bird feeding, understanding of the ecological effects of these massive subsidies is minimal. While bird feeding can bring positive benefits, such as increased overwinter survival and enhanced breeding success, there are also a number of potential negative impacts. For example, aggregations of birds around feeders may attract predators or enhance the spread of diseases. Feeders may also act as ecological traps, by providing inaccurate cues regarding habitat quality based on potential food resources.

Experimental studies investigating the potential impacts of supplementary feeding have dealt with a range of species, from small passerines (Figure 1) to birds of prey. Directed feeding experiments do not reflect the large-scale, diffuse nature of backyard feeding, but may provide some indication of the wider impacts. The form of supplementary feeding varies markedly among studies, replicates are few, and treatments often run consecutively, sometimes as single-site, before-and-after comparisons. As a result, meta-analysis of this disparate body of research is challenging. To focus advice and future research, we have drawn together and reviewed the many and varied responses of bird populations to supplementary feeding (Table 1). We begin with the effects on avian demography, starting with egg laying, and then progress through the avian life cycle to effects on adult survival. Finally, we consider the implications for adult behavior, species interactions, and indirect, community-level effects.

In a nutshell:

- Feeding birds is an enormously popular activity that can affect virtually every aspect of bird ecology, from daily survival to large-scale migration
- Supplementary feeding has the potential to effect long-term changes in the population dynamics and distribution of some bird species
- Although feeding birds generates mostly positive effects, some negative impacts, such as increased predation pressure and disease transmission, have also been observed
- Research is required on the wider impacts of feeding and on the interactions between food supply and factors such as climate and predation

[1]*School of Biological Sciences, Queen's University Belfast, Belfast, UK;* [2]*Central Science Laboratory, Sand Hutton, York, UK;* [3]*British Trust for Ornithology, The Nunnery, Thetford, Norfolk, UK;* [4]*Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Penryn, UK* [*]*(s.bearhop@exeter.ac.uk)*

Egg laying

The acute need for energy during egg development and laying means that supplementary feeding is likely to affect

avian fecundity and resource allocation during reproduction. During the breeding season, time is constrained, and even small shifts toward earlier laying usually bring benefits. In 34 of 59 studies in which laying dates were noted, feeding produced significantly earlier laying dates (Table 2). Such advances were generally less than one week, but, in some cases, were as long as one month. In most instances, earlier broods survive better than late ones (Barba *et al.* 1995), and extra food has the greatest impact when times are tough (eg in cold years [Svensson and Nilsson 1995], on low-quality territories, and in younger birds [Desroachers 1992]). The type of supplement provided also influences timing. For example, in one study, Florida scrub jays (*Aphe-locoma caerulescens*) given a high-fat, high-protein diet were first to lay, while those on high-fat, low-protein supplements came second, and control groups were unaffected (Reynolds *et al.* 2003). However, the same species also demonstrates the potential costs of an artificially influenced egg-laying time that becomes mismatched with natural food supply. Scrub jays breeding in suburban habitat with access to supplementary food breed earlier, but find themselves out of sync with natural food items that are important when rearing nestlings, potentially leading to decreased rather than increased breeding success (Schoech and Bowman 2001).


Courtesy of JJ Kennedy

Figure 1. *Great tit* (Parus major) *on a peanut feeder.*

Table 1. Summary of studies and the various impacts of supplementary feeding on breeding success

Type	*Lay date*		*Clutch size*		*Egg size/ quality*		*Incubation time*		*Hatching success*		*Chick growth rate*		*Fledging success*	
Birds of prey	+	7	+	6	+	1	+	na	+	1	+	2	+	6
	–	na	–	na	–	na	–	na	–	na	–	na	–	na
	None	3	None	3	None	3	None	na	None	2	None	5	None	4
Corvids	+	7	+	2	+	2	+	na	+	3	+	3	+	6
	–	na	–	na	–	na	–	na	–	na	–	na	–	na
	None	1	None	6	None	3	None	na	None	1	None	1	None	1
Small passerines	+	18	+	12	+	4	+	2	+	3	+	7	+	10
	–	1	–	na	–	na	–	na	–	na	–	na	–	na
	None	9	None	20	None	14	None	5	None	7	None	6	None	9
Seabirds	+	na	+	4	+	3	+	na	+	2	+	3	+	4
	–	na	–	na	–	na	–	na	–	na	–	1	–	na
	None	7	None	4	None	1	None	2	None	2	None	2	None	2
Waders/ waterfowl	+	2	+	4	+	3	+	na	+	na	+	2	+	2
	–	na	–	1	–	na	–	na	–	na	–	na	–	na
	None	4	None	1	None	2	None	na	None	na	None	na	None	na
Total	+	34	+	28	+	14	+	2	+	9	+	17	+	28
	–	1	–	1	–	0	–	0	–	0	–	1	–	0
	None	24	None	34	None	23	None	7	None	11	None	12	None	16

Notes: + = positive response; – = negative response; none = no impact; see WebPanel 1 for list of studies included in this summary.

Table 2. Summary of studies and the various impacts of supplementary feeding on breeding success

Breeding parameter	Response to supplemental food: % positive (n)		% negative (n)		% no effect (n)	
Lay date	57.6	(34)	1.7	(1)	40.7	(24)
Clutch size	44.4	(28)	1.6	(1)	54.0	(34)
Egg size/quality	37.8	(14)	0.0	(0)	62.2	(23)
Incubation time	22.2	(2)	0.0	(0)	77.8	(7)
Hatching success	45.0	(9)	0.0	(0)	55.0	(11)
Chick growth rate	56.7	(17)	3.3	(1)	40.0	(12)
Fledging success	63.6	(28)	0.0	(0)	36.4	(16)

Notes: n = number of studies reviewed; impacts included only examples in which statistically significant results are reported. A full data account with references is available in WebPanel 1.

Quantity and quality

Just as feeding affects the timing of laying, other breeding parameters, such as the number of eggs laid and their size and composition, can also be determined by diet and food availability. Because the size of clutches is subject to phylogenetic constraints and is known to decrease as the season progresses, resolving the effects of earlier laying from direct effects on clutch size is difficult. However, in 44 provisioning studies that dealt with both laying dates and clutch size, 12 reported increases in both, while 16 reported increases in clutch size alone (Table 2).

Supplemented birds may invest in larger or higher quality eggs as an alternative (or in addition) to investing in increased clutch size. Larger eggs are more likely to hatch and cool more slowly when adults are away from the nest (Mackintosh and Briskie 2005). Although egg size is considered a less plastic trait than lay date or clutch size, increases in egg size were reported in 38% of the studies we reviewed (Table 2); for example, fed Nazca boobies (*Sula granti*) laid substantially larger second eggs with heavier chicks than boobies that were not fed (Clifford and Anderson 2001). Nonetheless, increased egg size does not always lead to increased chick growth rate or survival, suggesting that, for some species, the benefits of increased egg size may be relatively short-lived and confined to the initial pre-and post-hatching period (Svensson and Nilsson 1995).

The effects of supplementary feeding on egg quality have also been reported for several species, and here again, Florida scrub jays have proven excellent models. Female jays provided with high-fat, high-protein supplements were found to lay heavier third eggs, containing more water and protein than the eggs of unsupplemented birds (Reynolds *et al.* 2003). Many popular supplemental foods (eg peanuts) are also known to be rich sources of macronutrients (such as vitamin E) and birds may benefit from increased uptake of specific nutrients with limited availability in the natural environment. These nutrients have been shown to affect measures of immunocompetence (the capacity to produce an immune response) and breeding parameters (Blount *et al.* 2002). For example, female lesser black-backed gulls (*Larus fuscus*) supplemented with high levels of carotenoids have been shown to lay higher quality eggs and are also more likely to produce replacement clutches following the removal of first clutches (Blount *et al.* 2002). The relative importance of energy versus specific nutrients in driving the effects of supplementary feeding could be investigated relatively easily, by manipulating both the energetic and macronutrient content of supplements.

Provisioning during breeding may extend the season by allowing birds to lay early, decreasing the time needed to raise chicks to fledging, and shortening the interval between clutches (Verboven *et al.* 2001), potentially allowing more pairs to rear second broods. When given food after their first clutch, second broods were initiated by all female black-throated blue warblers (*Dendroica caerulescens*) in the first year of feeding and by 67% of females in the second year, whereas only half of control pairs produced second broods in the first year and none did so in the second (Nagy and Holmes 2005).

The carry-over effect

There is evidence that effects on both lay date and clutch size are carried over to the year following supplementation. Ural owls (*Strix uralensis*) given supplementary food in one year layed one week earlier the following spring and also produced larger clutches (Brommer *et al.* 2004). In contrast, provisioning blue tits (*Cyanistes caeruleus*) in one year was shown to delay lay date the following year (Grieco *et al.* 2002).

Brood sex ratio

In birds, females are the heterogametic sex (ie they have two different sex chromosomes) and there is evidence that they are able to control the sex ratio of their offspring at the fertilization stage (Komdeur *et al.* 1997). Changes in food supply may therefore interact with the selective advantages of having male or female offspring. Adaptive sex ratio manipulation driven by food supplements generated a crisis in the conservation of the kakapo (*Strigops habroptilus*), a flightless parrot endemic to New Zealand. Reduced to a population of fewer than 70 individuals, supplementary feeding was initiated in an attempt to increase the productivity of female kakapos. Although feeding did increase fecundity rates, resulting sex ratios were strongly male-biased over several years, until it was realized that diet quality was influencing the sex ratio of chicks, and the diet was then altered to address the imbalance (Robertson *et al.* 2006). By contrast, in Tengmalm's owls (*Aegolius funereus*), the sex ratio of chicks was unaffected by additional feeding (Hörnfeldt *et al.* 2000), possibly because the impact of supplementary feeding may have been suppressed by high

natural food availability. Reduced effects of supplementary feeding during periods of high natural prey availability may help to explain the wide variability among studies.

Survival of young

The provision of additional food may allow breeding females to spend less time foraging, thereby allowing earlier initiation of incubation, better protection of eggs from predation, and earlier fledging, which can lead to higher survival rates (Bollinger *et al.* 1990). Supplementation during the laying-to-hatching period has been shown to increase both parental attendance and hatching asynchrony in Australian reed warblers (*Acrocephalus australis*; Eikenaar *et al.* 2003). Increased hatching asynchrony may itself bring benefits by spreading the time of peak food demand by chicks over a wider period.

Supplemented parents generally have a choice of either using extra food to maximize the delivery of natural prey to their chicks or to reduce foraging effort. In addition, extra food can facilitate more selective foraging (Grieco 2002). Generally, parents opt simply to reduce their foraging effort; however, the differing responses of males and females to supplementation highlight the distinct roles of the sexes during breeding. For example, female American kestrels (*Falco sparverius*) brought substantially less wild prey to their chicks when extra food was provided within nest boxes, but male provisioning was unaffected (Dawson and Bortolotti 2002); in addition, female European kestrels (*Falco tinnunculus*) made more use of the supplementary food themselves (Wiehn and Korpimäki 1997).

When supplementary food provided to parents was passed on to chicks, growth rates of chicks were positively impacted in 56% of the studies we reviewed. Surprisingly, however, one study of parasitic jaegers (*Stercorarius parasiticus*) identified a negative effect on chick growth. The authors suggest two possible explanations. First, the supplement may have been of poorer quality than natural food. Alternatively, parents in inferior condition may have depended more heavily upon the supplementary food, and the correlation between reduced growth rate and supplementary food intake may have been driven by lower parental quality and foraging ability (Davis *et al.* 2005).

Providing nestlings with additional supplementary food may also lead to a reduction in aggression among chicks, thereby increasing the survival of young, as has been observed in Spanish imperial eagle chicks (*Aquila adalberti*; González *et al.* 2006). Other studies have reported opposing results; feeding did not reduce sibling aggression in great egret (Casmerodius albus) or great blue heron (*Ardea herodias*) broods, though overall brood mortality was reduced by the addition of food through the enhancement of survival rates in smaller chicks (Mock *et al.* 1987).

Not surprisingly, the positive impacts of feeding on the survival of young have found practical application in enhancing the recovery of threatened species. The stitchbird (*Notiomystis cincta*), an endangered New Zealand species, has benefited considerably from provisioning, through both increased survival of young and increased productivity. However, at least in the short term, the persistence of these vulnerable island populations may depend upon the continued provision of supplemental food (Castro *et al.* 2003).

Ultimately, chicks given supplementary food were more likely to fledge than unsupplemented chicks in 64% of the studies we reviewed. In some cases, the effects were dramatic. Black-legged kittiwakes (*Rissa tridactyla*) given food over 2 years fledged twice as many chicks in the first year and three times as many in the second year (Gill and Hatch 2002). For kittiwakes, the timing of food provision was also found to be important in affecting fledging success: pairs fed throughout the breeding season and, from egg laying onward, had higher fledging success than those provisioned only during the pre-laying and laying stages. Other studies have found that supplementation reduced fledging success due to higher population densities in the provisioned area (Jansson *et al.* 1981). In that instance, feeders may act as ecological traps, encouraging birds to settle in an area with insufficient natural food during the breeding season, once supplementation has ended (ie feeders create a population level that cannot be sustained by natural levels of food). There is a clear need for more research into this possibility, by manipulation of the amount of food and the period over which food is provided.

Behavior

Given that food availability is one of the most important mediators of intra- and interspecific interactions among birds, particularly during the non-breeding season, it is not surprising that supplementation can influence behavior at a number of levels. The availability of food may influence the social behavior of birds when foraging. For example, supplementary food reduced the degree to which varied tits (*Poecile varius*) joined mixed-species flocks (Kubota and Nakamura 2000), supporting the hypothesis that mixed flocking helps birds find food in times of scarcity.

Food supplementation should also produce changes in territorial behavior, since this trait is often coupled with resource availability. During winter, flocks of black-capped chickadees defend foraging territories; however, this system often falls apart when food supplements are provided, as flocks frequently cross territorial boundaries to visit feeders (Wilson 2001). Alternatively, territorial behavior can increase with provisioning as the presence of clumped or high-quality food allows birds to engage in costly resource defense behaviors. When provided with food, Carolina wrens (*Thryothorus ludovicianus*) spend more time defending territories by singing (Strain and Mumme 1998). One of the most likely explanations for these differences among territorial responses to supplements is the defensibility of the resource, as food presented in small amounts in multiple areas will give the opportu-

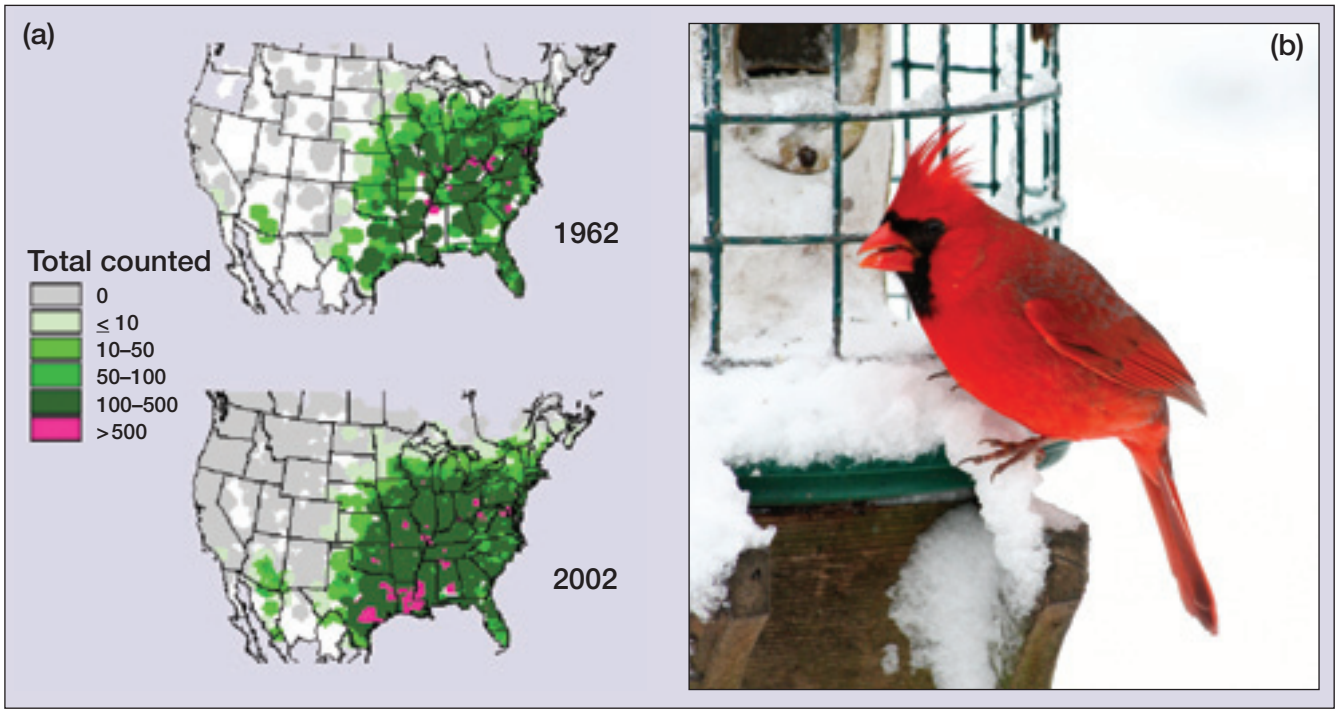

Figure 2. *(a) Range expansion of the northern cardinal over a 40-year period. The number of households participating in bird feeding has increased rapidly since the 1970s and expansion in the ranges of many species, such as the northern cardinal, is thought to be partially attributable to the presence of supplemental food. Data obtained from the National Audubon Society Christmas Bird Count historical results (2002), available at www.audubon.org/bird/cbc. (b) Northern cardinal* (Cardinalis cardinalis) *on feeder.*

nity for larger or more aggressive individuals to dominate the food supply. For example, older adult Egyptian vultures (*Neophron percnopterus*) exclude younger birds when individual carcasses are provided. However, when food is provided in a more scattered fashion, individuals can no longer defend the supply and no age group dominates feeding (Meretsky and Mannan 1999).

Supplementary feeding can also lead to changes in reproductive behavior, and feeding experiments provide a tool for testing theory relating the evolution of mating systems to food availability. For example, providing additional food to house sparrows (*Passer domesticus*) led to changes in female behavior that allowed mates to spend more time together at the nest and thereby reduced levels of extra-pair paternity (Václav *et al.* 2003).

■ Adult survival and range expansion

One of the most intuitive outcomes of overwinter feeding is that it should enhance survival. Indeed, this is probably the main reason that householders provide food for birds. Although survival rates of small passerines are hard to estimate, this expectation is borne out in several experiments showing higher survival probabilities among supplemented populations of species such as willow tits (*Parus montanus*) and crested tits (*Lophophanes cristatus*; Jansson *et al.* 1981). This work represents one of the few examples of diffuse, large-scale supplementary feeding that replicates the manner in which people actually feed birds in their back gardens, and is particularly valuable in that it provides contrast to the direct feeding of targeted individuals that characterizes most studies of supplementary feeding.

Supplementary food may also be responsible for large-scale changes in bird population dynamics and migration strategies, although it is clearly very difficult to make such causal links in an unequivocal manner. The northward expansions of the northern cardinal (*Cardinalis cardinalis*) and American goldfinch (*Carduelis tristis*) in the US (Morneau *et al.* 1999) are probably linked to backyard feeding (Figures 2 a,b). Feeding could also be responsible for the increasing tendency for birds to overwinter in Finland rather than migrating south (Jokimäki *et al.* 1996). Such changes may also bring large-scale dependency, and in Finland it is thought that some great tit populations are so dependent on supplementary food during winter that they can no longer be sustained by natural food sources alone (Orell 1989), highlighting the need for a greater understanding of the ways in which feeding may create ecological traps. However, there are examples that indicate otherwise: survival rates of black-capped chickadees following the cessation of 25 years of feeding did not differ from those of chickadees in areas where no feeders had been present (Brittingham and Temple 1992).

Few studies have been conducted on non-target species or on the impacts of supplementary feeding at a community level. While individuals that regularly use feeders are almost certainly reaping benefits, there may be negative impacts on other populations. Overwinter feeding can increase the number and density of resident birds that are attracted to an area and remain there to breed (Jansson *et al.* 1981).

Similarly, corvids (jays, crows, and allies, such as magpies and nutcrackers) living close to settlements spend 75% of their foraging bouts on anthropogenic food sources, and this appears to be linked to population increases (Marzluff 2006). This, in turn, could generate increased predation pressure on other birds, as corvids are known egg predators. In the case of small woodland passerines, high population densities at the end of winter could create competition for ecologically similar migrants returning to those areas during the breeding season, and urbanized areas in particular may eventually be dominated by a reduced number of species, assisted partly by their successful adaptation to artificial food source regimes (Cleargeau *et al.* 1998).


Courtesy of M Ruddock

Figure 3. *Hen harrier* (Circus cyaneus) *chick. Provisioning hen harrier nests with supplemental food was found to reduce the number of red grouse chicks caught by adult harriers to feed their chicks (Redpath 2001).*

■ Indirect ecological effects

The diseases that birds carry have been of considerable concern in recent years and the role that feeders may play in disease transmission has been highlighted, particularly for pathogens such as *Mycoplasma gallisepticum* or *Salmonella*. In the UK, this has led to the establishment of the *Garden bird health initiative*, which includes guidelines for feeding to help reduce the spread of disease as well as for the promotion of research into this area.

Disease transmission appears to vary according to the type of feeder used, the number of birds visiting it, and the habitat in which the feeder is located. In a survey of households in Wisconsin, bird mortality was found to be higher around platform feeders (Brittingham and Temple 1986). Bird feeders have also been implicated in the rapid spread of mycoplasmal conjunctivitis through the house finch (*Carpodacus mexicanus*) population in the US (Fischer *et al.* 1997). Importantly, these examples consider feeders used by the general public rather than small-scale experiments conducted by researchers and, as such, the findings may be more directly relevant to the actual impacts of feeder-related disease transmission.

While feeding may directly influence survival by reducing the risk of starvation, a similar effect might also be mediated through reduction of predation risk. Birds optimize their mass according to the trade-off between the risks of starvation (leading to fat storage) and predation (leading to maintenance of lower mass for quicker escape from predators; Lima 1986). Consistently provisioning a site decreases the perceived starvation risk, shifting the trade-off toward minimizing predation risk and reducing body mass (Gosler 1996).

A serious concern of householders is that birds at feeders may be exposed to increased predation risk, as predators might capitalize on aggregations around feeders. But surprisingly, research has shown that birds at feeders do not appear to bear a higher risk of predation (Dunn and Tessaglia 1994). Where population densities are high, the risk to individual birds is reduced via dilution and/or increased vigilance, and the presence of feeders has been associated with lower levels of predation by domestic cats (Woods *et al.* 2003). Perhaps most compellingly, Zanette *et al.* (2003) found that food supplementation had a greater effect on reproductive success in song sparrows when combined with low predator pressure than when predation and food supply were manipulated independently. A final mechanism by which feeding may reduce predation rates is by provisioning the predators themselves; for example, provisioning breeding hen harriers (*Circus cyaneus*, a raptor found in northern parts of Eurasia and North America) at the nest substantially reduced the number of red grouse (*Lagopus lagopus scoticus*) chicks delivered by harrier adults to feed their chicks (Redpath *et al.* 2001; Figure 3).

Feeding also has the potential to initiate trophic cascades, affecting the distribution and abundance of both prey and predator species. Increasing the number of birds around feeders can lead to hyperpredation of natural prey items in the immediate area (Martinson and Flaspohler 2003). Cascades driven by food provisioning could have serious consequences for some species. However, there have been very few studies on this phenomenon, probably because detecting and identifying cascading effects is notoriously difficult (Borer *et al.* 2005).

■ Conclusions

The popularity of backyard bird feeding is a relatively new phenomenon, but one that has increased markedly over the past three decades. Householders in the US and the UK purchase 500 000 tonnes of birdseed annually (O'Leary and Jones 2006) – enough to support almost

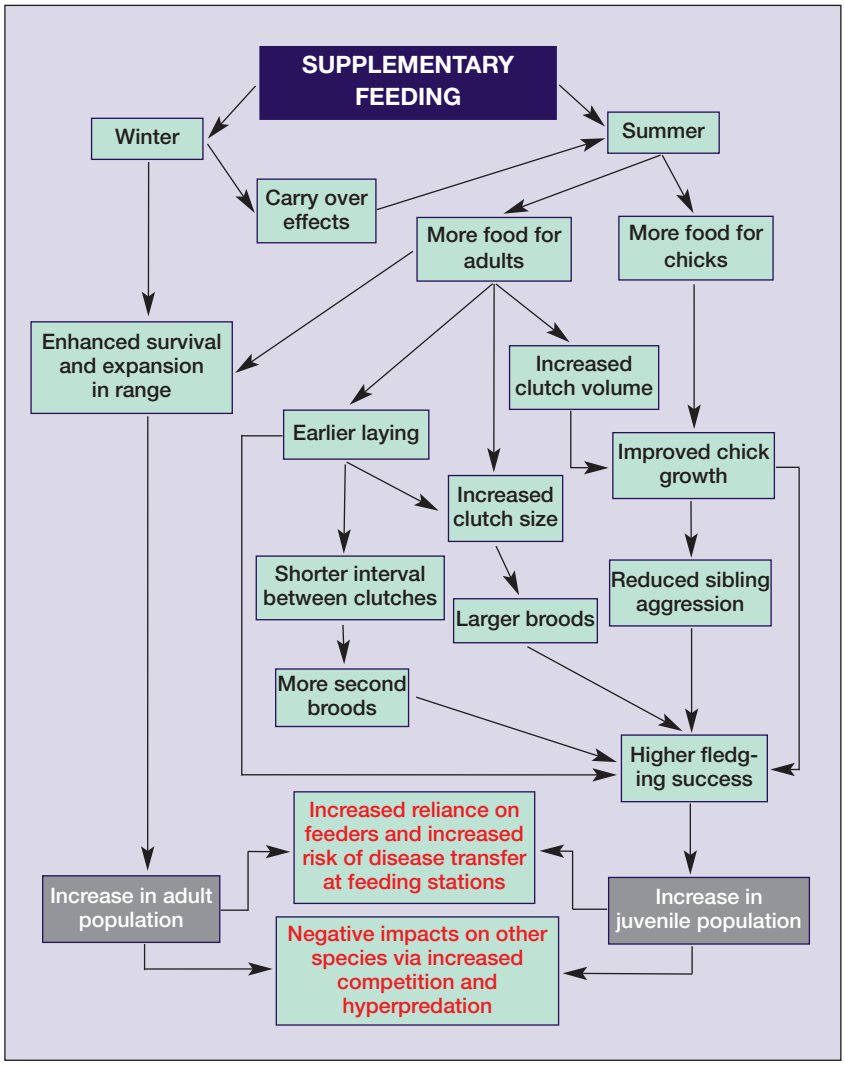

Figure 4. *Impacts of supplementary feeding on the population dynamics of birds. The potential impacts of supplementary feeding during winter and the summer breeding season are shown above, with arrows indicating the direction of the influence. The overall impact upon the population – an increase in both adult and juvenile numbers – is shown by the gray boxes. Negative impacts are shown in red.*

300 million chickadees feeding on nothing else per year (calculated from daily energy expenditures, based on data in Nagy *et al.* 1999). This growing market is worth an estimated US$4.5 billion in the US (Fair 2006) and £150–180 million in the UK (Toms 2003). Feeders allow an increasingly urbanized population to "get up close" to nature and, by doing so, may inspire more interest in conservation issues. Irrespective of their ecological impacts, feeders have enormous educational and social value (Cohn 2002).

Assessing the ecological impacts remains a formidable challenge. Until now, much of the research in this area has focused on assessing the impact of supplementation as a single factor. However, interactions between food supply and additional factors, such as predation or weather, will help to explain the variable conclusions among the studies we reviewed. Such work may also help us to understand how bird populations might respond to environmental change. While the consequences of interactions between food and weather as winter weather conditions shift with climate change may be revealed by well-designed feeding experiments, the importance and impact of anthropogenic interventions in food supply will also shift.

Experimentation with feeding remains problematic for several reasons. First, natural food is not always limiting, and so, in a mild winter, the addition of extra food may not make any difference to the targeted beneficiaries. Temporal variations of this nature do not diminish the importance of supplements: even if supplementation has an effect only once every few years, it may still exert a substantial influence on the demographics of a population. This highlights the importance of running experiments over multiple years in varying natural conditions. The effects of provisioning clearly differ according to the temporal and spatial scale of treatments and evidence of carry-over effects also indicates the merits of long-running, multi-seasonal observations at multiple sites.

While failure to publish non-significant results may create bias in reporting effects of supplementary feeding, the impacts at a population level are usually positive (Figure 4). Assessing individual variation in resource use and the extent to which supplements are used by individual birds may add considerable statistical noise to feeding treatments. If some individuals are relying heavily on supplemental food and benefiting, while others are consuming only a small amount and gaining little benefit, there may be variation in the impacts on the population that can be explained only through knowledge of individual resource use. One possible solution is to calculate the proportion of supplementary food in the diet of individuals using stable isotope analysis (Davis *et al.* 2005). Many of the foodstuffs that are fed to garden birds are likely to have stable isotope signatures that are distinct from "natural" foods. If supplements are not distinct, then there is also the option of using isotopic labels, which would make it possible to trace the uptake of even very small amounts of supplementary food.

Domestic bird feeding is widely perceived as a positive activity and is likely to benefit many species, including some of conservation concern, but we still have only a relatively basic understanding of how it affects bird populations. There are clearly a number of negative impacts that feeding may have, such as the creation of feeder-dependent birds and/or

ecological traps, the spread of disease, or exposure to increased predation rates. Some of these concerns may be mitigated by following one of the many "good practice" feeding guidelines currently available (eg Project Feeder Watch 2007), but such advice is usually based on very few scientific studies. Small-scale supplementary feeding experiments give us some indication of the impacts that may result from widespread backyard feeding. But what is really needed are more large-scale, diffuse provisioning experiments that mimic more closely the manner in which households feed birds. While the available evidence supports the substantial and broadly positive role of feeding birds in avian conservation and increased public awareness of wildlife, assessing the wider impacts of supplementary feeding by well-meaning and big-spending households merits a considerable research effort from ecologists.

Acknowledgements

Funding was provided through a Department for Employment and Learning research studentship to GR.

References

Barba EL, Gildelgado JA, and Monros JS. 1995. The costs of being late – consequences of delaying great tit *Parus major* first clutches. *J Anim Ecol* **64**: 642–51.

Blount JD, Surai PF, Nager RG, *et al.* 2002. Carotenoids and egg quality in the lesser black-backed gull *Larus fuscus*: a supplemental feeding study of maternal effects. *Proc R Soc Lond B Bio* **69**: 29–36.

Bollinger PB, Bollinger EK, and Malecki RA. 1990. Tests of three hypotheses of hatching asynchrony in the common tern. *Auk* **107**: 696–706.

Borer ET, Seabloom EW, Shurin KE, *et al.* 2005. What determines the strength of a trophic cascade? *Ecology* **86**: 528–37.

Brittingham MC and Temple SA. 1986. A survey of avian mortality at winter feeders. *Wildlife Soc B* **14**: 445–50.

Brittingham MC and Temple SA. 1992. Does winter bird feeding promote dependency? *J Field Ornithol* **63**: 190–94.

Brommer JE, Karell P, and Pietiäinen H. 2004. Supplementary fed Ural owls increase their reproductive output with a one year time lag. *Oecologia* **139**: 354–58.

Castro I, Brunton DH, Mason KM, *et al.* 2003. Life history traits and food supplementation affect productivity in a translocated population of the endangered hihi (stitchbird, *Notiomystis cincta*). *Biol Conser* **114**: 271–80.

Cleargeau P, Savard J-PL, Mennechez G, and Falardeau G. 1998. Bird abundance and diversity along an urban–rural gradient: a comparative study between two cities on different continents. *Condor* **100**: 413–25.

Clifford LD and Anderson DJ. 2001. Food limitation explains most clutch size variation in the Nazca booby. *J Anim Ecol* **70**: 539–45.

Cowie RJ and Hinsley SA. 1988. The provision of food and the use of bird feeders in suburban gardens. *Bird Study* **35**: 163–68.

Davis SE, Nager RG, and Furness RW. 2005. Food availability affects adult survival as well as breeding success of parasitic jaegers. *Ecology* **86**: 1047–56.

Dawson RD and Bortolotti GR. 2002. Experimental evidence for food limitation and sex-specific strategies of American kestrels (*Falco sparverius*) provisioning offspring. *Behav Ecol Sociobiol* **52**: 43–52.

Desroachers A. 1992. Age-related differences in reproduction by European blackbirds – restraint or constraint. *Ecology* **73**: 1128–31.

Dunn EH and Tessaglia DL. 1994. Predation of birds at feeders in winter. *J Field Ornithol* **65**: 8–16.

Eikenaar C, Berg ML, and Komdeur J. 2003. Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian reed warbler *Acrocephalus australis*. *J Avian Biol* **34**: 419–27.

Fair J. 2006. Should we feed birds? *BBC Wildlife* **24**: 46–48.

Fischer JR, Stallknecht DE, Luttrell MP, *et al.* 1997. Mycoplasmal conjunctivitis in wild songbirds: the spread of a new contagious disease in a mobile host population. *Emerg Infect Dis* **3**: 69–72.

Gill VA and Hatch SA. 2002. Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding. *J Avian Biol* **33**: 113–26.

González LM, Margalida A, Sánchez R, and Oria J. 2006. Supplementary feeding as an effective tool for improving breeding success in the Spanish imperial eagle (*Aquila adalberti*). *Biol Conserv* **129**: 477–86.

Gosler A. 1996. Environmental and social determinants of winter fat storage in the great tit *Parus major*. *J Anim Ecol* **65**: 1–17.

Grieco F. 2002. How different provisioning strategies result in equal rates of food delivery: an experimental study of blue tits *Parus caeruleus*. *J Avian Biol* **33**: 331–41.

Grieco F, van Noordwijk AJ, and Visser ME. 2002 Evidence for the effect of learning on timing of reproduction in blue tits. *Science* **296**: 136–38.

Hörnfeldt B, Hipkiss T, Fridolfsson AK, *et al.* 2000. Sex ratio and fledging success of supplementary-fed Tengmalm's owl broods. *Mol Ecol* **9**: 187–92.

Jansson C, Ekman J, and Von Brömssen A. 1981. Winter mortality and food-supply in tits *Parus*-spp. *Oikos* **37**: 313–22.

Jokimäki J, Suhonen J, Inki K, and Jokinen S. 1996. Biogeographical comparison of winter bird assemblages in urban environments in Finland. *J Biogeogr* **23**: 379–86.

Komdeur J, Daan S, Tinbergen J, and Matemans C. 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. *Nature* **385**: 522–25.

Kubota H and Nakamura M. 2000. Effects of supplemental food on intra and inter-specific behaviour of the varied tit *Parus varius*. *Ibis* **142**: 312–19.

Lima SL. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67**: 377–85.

Mackintosh MA and Briskie JV. 2005. High levels of hatching failure in an insular population of the South Island robin: a consequence of food limitation? *Biol Conserv* **122**: 409–16.

Martinson TJ and Flaspohler DJ. 2003. Winter bird feeding and localized predation on simulated bark-dwelling arthropods. *Wildlife Soc B* **31**: 510–16.

Marzluff JM and Neatherlin E. 2006. Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation. *Biol Conserv* **130**: 301–14.

Meretsky VJ and Mannan RW. 1999. Supplemental feeding regimes for Egyptian vultures in the Negev Desert, Israel. *J Wildlife Manage* **63**: 107–15.

Mock DW, Lamey TC, and Ploger BJ. 1987. Proximate and ultimate roles of food amount in regulating egret sibling aggression. *Ecology* **68**: 1760–72.

Morneau F, Decarie R, Pelletier R, *et al.* 1999. Changes in breeding bird richness and abundance in Montreal parks over a period of 15 years. *Landscape Urban Plan* **44**: 111–21.

Nagy KA, Girard IA, and Brown TK. 1999. Energetics of free-ranging mammals, reptiles, and birds. *Annu Rev Nutr* **19**: 247–77.

Nagy LR and Holmes RT. 2005. Food limits annual fecundity of a migratory songbird: an experimental study. *Ecology* **86**: 675–81.

Newton I. 1998. Population limitation in birds. London, UK: Academic Press Limited.

O'Leary R and Jones D. 2006. The use of supplementary foods by Australian magpies *Gymnorhina tibicen*: implications for wildlife feeding in suburban environments. *Austral Ecol* **31**: 208–16.

Orell M. 1989. Population fluctuations and survival of great tits *Parus major* dependent on food supplied by man in winter. *Ibis* **131**: 112–27.

Project Feeder Watch. 2007. About birds and bird feeding. www.birds.cornell.edu/pfw/AboutBirdsandFeeding/abtbirds_index.html. Viewed 30 May 2007.

Redpath SM, Thirgood SJ, and Leckie FM. 2001. Does supplementary feeding reduce predation of red grouse by hen harriers? *J Appl Ecol* **38**: 1157–68.

Reynolds SJ, Schoech SJ, and Bowman R. 2003. Nutritional quality of prebreeding diet influences breeding performance of the Florida scrub-jay. *Oecologia* **134**: 308–16.

Robertson BC, Elliott GP, Eason DK, *et al.* 2006. Sex allocation theory aids species conservation. *Biol Lett* **2**: 229–31.

Schoech SJ and Bowman R. 2001. Variation in the timing of breeding between suburban and wildland Florida scrub-jays: do physiologic measures reflect different environments? In: Marzluff JM, Bowman R, and Donnelly R (Eds). Avian conservation and ecology in an urbanizing world. New York, NY: Kluwer Academic.

Strain JG and Mumme RL. 1998. Effects of food supplementation, song playback, and temperature on vocal territorial behaviour of Carolina wrens. *Auk* **105**: 11–16.

Svensson E and Nilsson JA. 1995. Food supply, territory quality, and reproductive timing in the blue tit (*Parus caeruleus*). *Ecology* **76**: 1804–12.

Toms M. 2003. The BTO/CJ garden birdwatch book. Thetford, UK: British Trust for Ornithology.

Václav R, Hoi H, and Blomqvist D. 2003. Food supplementation affects extrapair paternity in house sparrows (*Passer domesticus*). *Behav Ecol* **14**: 730–35.

Verboven N, Tinbergen JM, and Verhulst S. 2001. Food, reproductive success and multiple breeding in the great tit *Parus major*. *Ardea* **89**: 387–406.

Wilson WH. 2001. The effects of supplemental feeding on wintering black-capped chickadees (*Poecile atricapilla*) in central Maine: population and individual responses. *Wilson Bull* **113**: 65–72.

Woods M, McDonald RA, and Harris S. 2003 Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Rev* **33**: 174–88.

Zanette L, Smith JNM, van Oort H, and Clinchy M. 2003. Synergistic effects of food and predators on annual reproductive success in song sparrows. *Proc R Soc Lond B Bio* **270**: 799–803.

Wiehn J and Korpimaki E. 1997. Food limitation on brood size: experimental evidence in the Eurasian kestrel. *Ecology* **78**: 2043–50.

